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CONTENTS

	PAGE
BEALL, Geoffrey, and WILLIAMS, C. B., M.A., Sc.D. Geographical variation in the wing length of <i>Danaus plexippus</i> (Lep. Rhopalocera)	65-76, 2 figs.
CARPENTER, Professor G. D. Hale, M.B.E., D.M., F.R.E.S. Notes by E. Burtt, B.Sc., F.R.E.S., on the habits of a species of <i>Oxyphilus</i> (MANTIDAE), and the flight of the male of a species of <i>Palophus</i> (PHASMIDAE)	82-83
FISHER, K. J. (Mrs. Richardson). Butterfly migration in Eastern Asia	77-81
KALMUS, H., D.Sc., M.D. Correlations between flight and vision, and particularly between wings and ocelli, in insects	84-96, 2 figs.
SCHWANWITSCH, B. N. Wing-pattern in Lycaenid Lepidoptera	97-100, 7 figs.
BOOK NOTICE	83

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GEOGRAPHICAL VARIATION IN THE WING LENGTH OF *DANAUS PLEXIPPUS* (LEP. RHOPALOCERA)

By Geoffrey BEALL¹

(Institute of Paper Chemistry, Appleton, Wisconsin)

and

C. B. WILLIAMS, M.A., Sc.D.

(Rothamsted Experiment Station, Harpenden).

1. Introductory.

A STUDY of the geographical variation in wing length of the monarch butterfly, *Danaus plexippus* L., was undertaken to discover whether there occurred such differences, within North America in particular, that a group of monarchs originating in one region might be distinguished from a group arising elsewhere. Such a decision turns, of course, on the variability of individual butterflies in a given region. It was anticipated that the groups to be compared would overlap

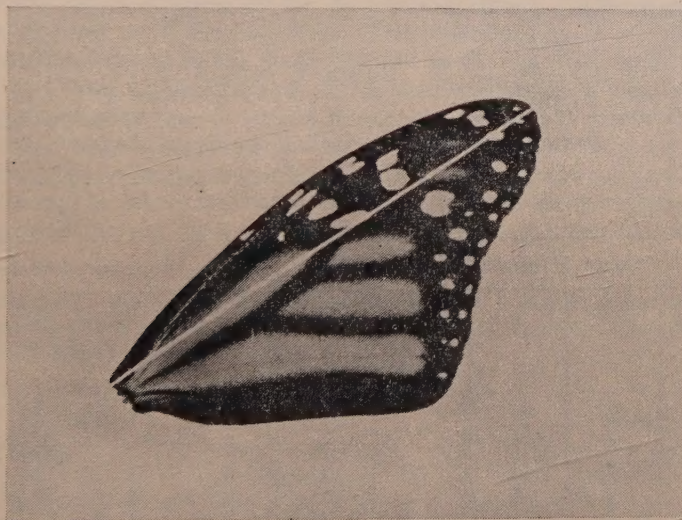


FIG. 1.—The length of the wing of the monarch butterfly.

but hoped that the regional effects would be sufficient to make differences in average value significant.

Data were collected by political divisions for the three main forms, *plexippus*, *erippus* and *nigrippus*, of *Danaus plexippus*, as shown below. As a convenient

¹ Formerly of the Division of Entomology in the Canadian Dominion Department of Agriculture. It was during this former service that much of the present data were collected.

character, the length of the right fore-wing, *i.e.*, the distance, indicated by the line in fig. 1, from the proximal costal corner to the most distant point in the apex, was measured to the nearest millimetre. In the case of specimens that could be dissected, the wing was detached, after some days of storage, and measured. In the case of museum material, the specimen was, of course, not broken up, but the length of the wing was found with dividers or with a simple optical device, described by Williams (1943), which can be used for set specimens without touching them and which gives exact measurement.

2. *Danaus plexippus plexippus* L.

The first form of *Danaus plexippus* to be considered is the typical *plexippus*, found exclusively in the colonies established outside America and almost exclusively in North America, as noted by Williams *et al.* (1942). Tables II and III are devoted, respectively, to data on this form from the two continental races of America and Australia, and Table I to races on remote islands.

Consider first the data from the remote islands of Guam, Formosa and the Canaries as shown in Table I. The butterflies here involved were all examined by C. B. Williams in the collections of the British Museum (Natural History) in London and at Tring. The frequency of occurrence of different lengths, in mm., of the fore-wing is shown by islands and by sexes. The number, *n*, of butterflies and the average length of the wing is shown below the primary data in each case.

TABLE I.

The frequency of occurrence of different lengths, in mm., of the fore-wing of *Danaus plexippus plexippus* L. from remote islands.

mm.	Females				Males			
	Guam	Formosa	Canaries	Total	Guam	Formosa	Canaries	Total
43							1	1
44							1	1
45			1	1		1		1
46						1		1
47			1	1	1	1	1	3
48	1		2	3	4		1	5
49	2	1		3	1		1	2
50	3	2	2	7	6	1	3	10
51	3	1		4	3	1		4
52	4			4	3	1		4
53	1			1	1	2		3
54	6			6	6			6
55	1			1		1		1
56					1			1
<i>n</i>	21	4	6	31	26	9	8	43
Average	51.9	50.0	48.0		51.2	50.2	47.6	

From Table I it can be seen at once that there is considerable variation within each island in the size of the butterflies but also a suggestion of overriding

regional variation. Statistical analysis ² shows that the variation between the islands is indeed very much greater than within the groups, *i.e.*, that the average values for the groups vary more than is to be expected from the variation within the groups. Obviously, the heterogeneity arises largely from the smallness of the butterflies in the Canaries. The monarch butterflies involved are presumably restricted to their islands rather than migrant like those of North America and hence the differences may be genetic. These data of Table I illustrate, however, the possibility of distinguishing, as a group, butterflies of one region from those of another by average size, in spite of considerable and overlapping local variation.

Consider next more extensive and various data from North America, by political subdivisions as shown in Table II. The Mexican material was measured by C. B. Williams, in his collection and in the British Museum. The Californian material was furnished, in part, by Professor Harry S. Smith, who with the greatest kindness sent to G. Beall a collection made in the winter of 1942 at Ventura by Dr. Paul de Bach and Dr. D. C. Lloyd. The other Californian material, measured by C. B. Williams, was collected by Messrs. A. Forbes, D. M. Duperu and J. A. Downes (in large part), particularly at Pacific Grove, during the 2 winter seasons in 1937-39. Two collections made during the autumns of 1938 and 1941 in Louisiana were most kindly contributed by Mr. Percy Viosca, Jr., of the Southern Biological Supply Co. of New Orleans and measured by G. Beall. The collections from Florida are museum material, belonging to C. B. Williams, taken from 1937 to 1942. The collection from Minnesota was made at Sedan by Mr. M. Denning from a "migrating swarm" in 1929, as reported by Williams (1938). The collections made in Ontario were taken during the autumn in the years 1935-43 at Pt. aux Pins, as described by Beall (1941). Table II, like Table I, shows the distribution of wing length and average length of wing.

From the average wing length in Table II, there appears to be some heterogeneity among the monarch butterflies of North America, not unlike that shown to exist between the islands indicated in Table I. The heterogeneity is the more interesting in the present case where the butterflies may undertake migrations

² The treatment appropriate to discover whether the variation between groups is greater than that within groups is, of course, the analysis of variance, which for the data of Table I is as follows:

Variability	Females			Males		
	<i>f</i>	Mean sq.	<i>F</i>	<i>f</i>	Mean sq.	<i>F</i>
Between groups . . .	2	36.46	9.95**	2	38.13	5.10*
Within groups . . .	28	3.66		40	7.47	

The details of the calculations involved here are indicated in an Appendix (p. 75). Here it may be noted that the ratio of the mean square (squared standard deviation) Between Groups to that Within Groups is indicated by the quantity, *F*. A value of *F* with a probability lying between 0.05 and 0.01, *i.e.*, a result possibly significant, is marked with a single asterisk while a value beyond 0.01, *i.e.*, a result very probably significant, is marked with a double asterisk. The probabilities are found by reference to the table of Snedecor (1934). From the size of *F* above, for both sexes it is plain that there is a significant difference in the mean size of butterflies from the various islands indicated in Table I.

TABLE II.

The frequency of occurrence of different lengths, in mm., of the fore-wing of
Danaus plexippus plexippus L. from North America.

mm.	Mexico	California	Louisiana	Florida	Minnesota	Ontario	Total
Females							
40		1					1
41							
42		1					1
43						1	1
44	1	2	1		1		5
45		1			1	3	5
46		3			2	6	11
47		2	1	1		6	10
48	4	8	3	1	3	20	39
49	2	17	4		1	26	50
50	6	13	8	1	2	54	84
51	1	17	9	3	2	83	115
52		12	7		1	122	142
53		13	1			107	121
54	1	5		1		65	72
55		3		1		32	36
56						10	10
57						2	2
<i>n</i>	15	98	34	8	13	537	705
Average	49.3	50.3	50.2	50.9	48.3	51.9	
Males							
43		2					2
44		2					5
45		6	4		1	2	13
46		7	3		1	5	16
47		9	2		1	8	20
48	4	18	2			6	30
49		22	3	3	4	25	57
50	4	31	13		2	48	98
51	3	30	18	2	3	72	128
52	2	34	13	3	7	101	160
53	4	20	9	2	2	113	150
54		10	3	1	3	75	92
55		5				46	51
56		1	1			19	21
57		1				2	3
58						1	1
59						1	1
<i>n</i>	17	198	71	11	26	525	848
Average	50.6	50.3	50.6	51.4	50.3	52.3	

that should tend to keep them uniform. This heterogeneity is statistically³ significant but depends to a considerable extent on the presence of material from Ontario—larger by 1 or 2 mm., on the average, than the other collections. The present result suggests that we should be able to distinguish populations arising in the Great Lakes region, or northward, from those arising elsewhere, particularly in the Great Plains, as represented by Minnesota. From these

TABLE III.

The frequency of occurrence of different wing lengths, in mm., of the fore-wing of *D. p. plexippus* L. from Australia.

mm.	Females				Males			
	Australia generally	Queens-land	N.S. Wales	Total	Australia generally	Queens-land	N.S. Wales	Total
44					1			1
45								
46	1			1				
47					1			1
48					1	1		2
49	1			1			1	1
50		2		2	1	1	2	4
51	4		1	5	3	2	1	6
52	1		4	5		1	1	2
53	2			2	2		1	3
54		1	2	3	2		2	4
55					1			1
<i>n</i>	9	3	7	19	12	5	8	25
Average	50.8	51.3	52.4		50.9	50.4	51.6	

data there is no indication of where the Ontarian monarchs go in the autumn and winter, when the southern collections were made, although it is curious that the material from Florida (south of Ontario) is bigger than that from Louisiana or California.

If the material of Table II is reconsidered with the Ontarian collections

³ The analysis of variance for the data of Table II is as follows:—

Variability	Females			Males		
	<i>f</i>	Mean sq.	<i>F</i>	<i>f</i>	Mean sq.	<i>F</i>
Between groups . . .	5	97.41	20.61**	5	135.13	26.15**
Within groups . . .	699	4.73		842	5.17	

It will be seen that the variability between groups is some 20 times as great (the *F* value) as within groups and such a result would arise very improbably by chance, hence the differences between groups are very clearly significant.

omitted, there is no statistical ⁴ assurance that the populations outside Ontario, in North America, are heterogeneous. There remains, however, a general over-all suggestion that size declines towards the south and the west but that the pre-eminence or heavy weighting of the observations for California and Louisiana may mask some heterogeneity.

Limited data on *D. p. plexippus* in Australia are shown in Table III. This material, like that of Table I, was examined by C. B. Williams in his private collection or in the collections of the British Museum. Some of the material was simply labelled—Australia. Some material was labelled as from the States of Queensland or New South Wales, although since so little is known of the migration of the monarch in Australia, we cannot say whether the specimens originated where they were caught.

From the average values shown in Table III it appears that the material from New South Wales is about 1 mm., bigger than that from Queensland although it is not sufficient to establish the point statistically.⁵ In so far as this effect exists, it corresponds to the American experience where Ontario in the high latitudes contributes the biggest butterflies.

3. *Danaus plexippus erippus* Cramer.

The second form of *Danaus plexippus* to be considered is *erippus* of, roughly, America south of the Amazon. Table IV is devoted to this form. The butterflies were all examined by C. B. Williams in his private collection, the collections of the British Museum or in the National Museum of Brazil at Rio de Janeiro.

From the average values of Table IV for *D. p. erippus* there is a suggestion that wing length tends to decrease towards the low altitudes and towards the

⁴ We may repeat the analysis of variance, excluding Ontario, with the following result :—

Variability	Females			Males		
	<i>f</i>	Mean sq.	<i>F</i>	<i>f</i>	Mean sq.	<i>F</i>
Between groups .	4	15.21	2.48*	4	3.72	
Within groups .	163	6.13		318	6.23	1.67

Now the values of *F* are not significant.

⁵ The analysis of variance of the data in Table III is as follows :—

Variability	Females			Males		
	<i>f</i>	Mean sq.	<i>F</i>	<i>f</i>	Mean sq.	<i>F</i>
Between groups .	2	5.40	1.54	2	2.48	
Within groups .	16	3.50		22	6.91	2.78

The values of *F* are not significant.

TABLE IV.

The frequency of occurrence of different lengths of the fore-wing of
Danaus plexippus erippus Cramer.

mm.	Brazil	Paraguay	Uruguay	Argentina	Chile	Total
Females						
34	1					1
35						
36						
37						
38	2	1				3
39	1					1
40	2	1		2		5
41					1	1
42				1		1
43	1	1		2	1	5
44	3	2	1	1	2	9
45	3			2		5
46	14			3	1	18
47	4	1		3		8
48	6		2	4		12
49	1			2		3
50	2			3		5
51				1		1
<i>n</i>	40	6	3	24	5	78
Average	45.2	42.7	46.7	46.3	43.6	
Males						
35	1					1
36						
37					2	2
38	1					1
39	1					1
40	1	1		1		3
41						
42	2	1		3	1	7
43	1				3	4
44	3	1	1		4	9
45	1	1	1		4	7
46	8	2		3	3	16
47	6	1		1	9	17
48	18			5	2	25
49	6			5	4	15
50	5		3	5		13
51	1	1	1			3
52	2			1		3
<i>n</i>	57	8	6	24	32	127
Average	46.8	45.1	48.3	47.4	45.4	

west, as is possibly the case in North America for *D. p. plexippus*. That there is heterogeneity from one group to another is statistically probable.⁶

4. *Danaus plexippus nigrippus*.

The third form of *Danaus plexippus* to be considered is *nigrippus* which occupies the northern part of South America and the West Indies, as shown by Williams *et al.* (1942), together with some specimens intermediate in coloration to the typical *plexippus*. The data on *nigrippus*, excluding any typical *plexippus*, are shown in Table V. The butterflies involved were all examined by C. B. Williams, in his own collection, the collections of the British Museum, and of the National Museum of Brazil.

From the average values shown in Table V it can be seen there is not much variation with place in the size of *D. p. nigrippus* as proves to be the case

TABLE V.

The frequency of occurrence of different lengths, in mm., of the fore-wing of *Danaus plexippus nigrippus*.

mm.	Brazil	Trinidad	British Guiana	Colombia	Ecuador	Peru	Dominica	Haiti	Total
Females									
38				1					1
39				1				1	2
40						1			1
41									
42				2			1		3
43		1				1			2
44	1	3	1	2					7
45	1			7	3	3			14
46	2	2	3	5	3	2	1		18
47		1	3	2	1	1	2	3	13
48	2		2	4		1	2	2	13
49		1	1	2	1	4	1		10
50				2					2
51				1					1
52				2					2
<i>n</i>	6	8	10	31	8	13	7	6	89
Average	46.2	45.4	46.8	46.2	46.1	46.2	46.7	46.0	

⁶ The analysis of variance from Table IV is as follows :—

Variability	Females			Males		
	<i>f</i>	Mean sq.	<i>F</i>	<i>f</i>	Mean sq.	<i>F</i>
Between groups .	4	21.92	2.12	4	24.31	2.47*
Within groups .	73	10.34		122	9.85	

For males the value of *F* has a probability between 0.05 and 0.01 and so is possibly significant. Considering simultaneously values of *F* the result is probably significant.

TABLE V.—continued.

mm.	Brazil	Trinidad	British Guiana	Colombia	Ecuador	Peru	Dominica	Haiti	Total
Males									
34						1			1
35									
36									
37									
38			1						1
39									
40					1				1
41		2							2
42									
43		1			1	1		1	4
44		3	1	3	1	1		1	10
45		1	1	2		1	2		7
46	2	7	1	3	3	3	1		20
47	1	2	3	7	2	5	1	1	22
48		3	2	5	4	3	4	2	23
49	1	1	3	2	3	1		3	14
50	3		3	3		3	5	2	19
51	1					1	1	1	4
52									
53						1			1
<i>n</i>	8	20	15	25	15	21	14	11	129
Average	48.6	45.6	47.1	47.1	46.5	47.0	48.3	48.0	

statistically.⁷ This result is the more surprising since *nigrippus* presumably does not migrate and so might have been expected to show more variation than, at least, the migrating typical *plexippus* of the north.

5. Discussion and Summary.

From the material presented, it can be seen that marked, *i.e.*, statistically significant, differences in average size of monarch butterflies (forms *plexippus* and *erippus*) occur in different regions both isolated, as in the remote islands, and also on the continents. Accordingly it can be seen that if one population should be replaced by another with an average wing length 1 mm. less—as might easily be the case in North America—that 2 successive samples of 50 butterflies would suffice to detect the change statistically.⁸ This result justifies

⁷ The analysis of variance from Table V is as follows:—

Variability	Females			Males		
	<i>f</i>	Mean sq.	<i>F</i>	<i>f</i>	Mean sq.	<i>F</i>
Between groups . . .	7	1.60		7	14.35	2.11*
Within groups . . .	81	7.09	4.44*	121	6.79	

Both values of *F* exceed the range to be expected by chance (0.05 probability) but the value is excessively small for females and excessively large for males. Considering both values of *F* the result is not significant.

⁸ It is assumed here that the mean square, or squared standard deviation, within groups be 5, as is approximately the case in the analysis of variance of North American data.

the hope that during migration a population from one region might be distinguished from a succeeding population that had originated elsewhere.

Although collections of any size from populations with an average difference as small as 1 mm. can be readily distinguished it would be most hazardous to attempt to distinguish single specimens on the same basis. The situation is well illustrated from the consideration of the two forms, *plexippus* the largest and *erippus* the smallest, considered in the present paper. Thus, in the present collections only 319 males of *plexippus* out of 848 exceed the highest value, 52

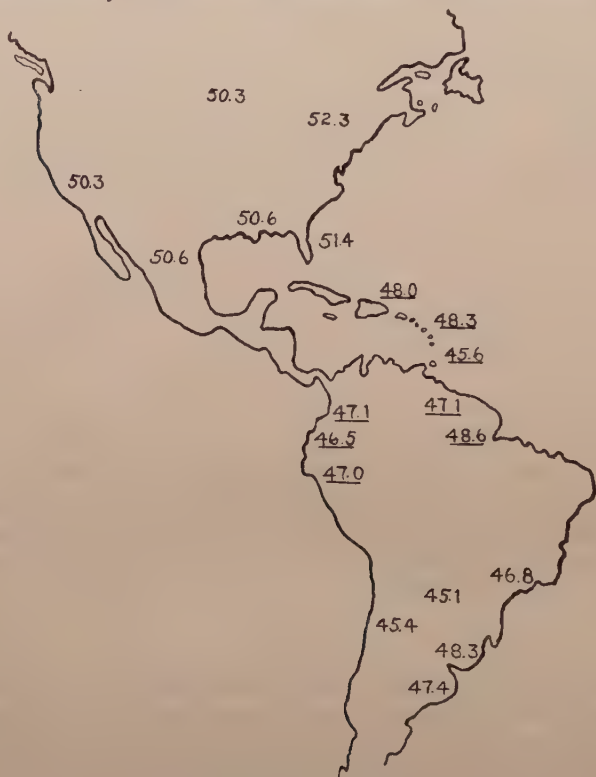


FIG. 2.—The mean length of fore-wing of male *Danaus plexippus* in America.

mm., found for *erippus* and 30 of *plexippus* fall below the average of 46.6 mm. for the southernmost form.

It has been suggested in various places that there is a tendency for the collections to have higher average values in the higher latitudes, and to illustrate this effect fig. 2 shows the average values of males in all collections made in America. The values for *nigrippus* are underlined so that the 3 forms may be distinguished. The affect of high latitude is reminiscent of the high yields of crops towards the Arctic limit of their range which has been illustrated for maize in North America by Jones and Huntingdon (1935). There is also in fig. 2 some suggestion of a longitudinal effect—smaller to the west—as previously mentioned.

The records involved in fig. 2 could be conveniently extended to New England and the upper Pacific States to test the validity of the apparent effects of latitude and longitude. If these collections were made in the autumn there

would be little question of the butterflies having originated to the south. The present investigation suffers from the disadvantage of our not knowing the place and time of breeding of the continental populations, except in a general way for the autumn migrants taken in Minnesota and Ontario of the north. It would be highly desirable if collectors could get local material, preferably by seasons, to replace the present material. Butterflies might be obtained from caterpillars taken in the field, but it might be more convenient to simply record butterflies taken within a day or two of emergence. Such butterflies can be distinguished, according to Clark (1941), by an ephemeral iridescence of the fore-wing. Records, of the sort indicated, are needed particularly from the southern United States.

Appendix on the analysis of variance

(by Geoffrey Beall).

The analysis of variance used in the preceding work was made on the lines indicated by Snedecor (1943: 13-14) and will be illustrated for the case of females in Table I. Let x_{ij} be the measurement on the i^{th} butterfly of j^{th} group containing n_j butterflies. Let there be m groups. Then first calculate a quantity Snedecor has termed the correction, *i.e.*,

$$C = \left(\frac{\sum_{j=1}^m \sum_{i=1}^{n_j} x_{ij}^2}{\sum_{j=1}^m n_j} \right) = \frac{(1577)^2}{31} = 80,223.5161,$$

where the numerator is simply the square of the sum of measurements and the denominator is the number of butterflies. Next calculate the total sum of squares (about mean) as

$$S_T = \sum_{j=1}^m \sum_{i=1}^{n_j} x_{ij}^2 - C = 80,399 - C = 175.4839,$$

where the sum of measurements squared is involved. Next calculate the sum of squares (about mean) between groups as

$$S_G = \frac{\sum_{j=1}^m \left(\sum_{i=1}^{n_j} x_{ij} \right)^2}{n_j} \\ = \frac{(1089)^2}{21} + \frac{(200)^2}{4} + \frac{(288)^2}{6} - C = 72.9125,$$

when 3 new quantities, similar to C , are involved. The analysis of variance is now:—

Variation	Freedom	Sum of squares	Mean square
Between groups . . .	$m - 1$	S_G	$S_G/(m - 1)$
Within groups . . .	$\sum_{j=1}^m n_j - m$	$S_T - S_G$	$(S_T - S_G)/(\sum_{j=1}^m n_j - m)$
Total . . .	$\sum_{j=1}^m n_j - 1$	S_T	

as has been previously numerically illustrated.

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BUTTERFLY MIGRATION IN EASTERN ASIA

By K. J. FISHER (Mrs. Richardson).

As a result of the work of Williams (1930) and the interest it aroused in the subject of butterfly migration, a considerable mass of information has accumulated, and the geographical aspects of the subject have not been neglected. By 1930, migrations had been recorded from almost every part of the tropical and temperate zones except from China and French Indo-China; in 1938, in spite of the great number of further observations made in other parts of the world, this important blank in Eastern Asia still remained unfilled.

In 1939, I went out to China by way of Saigon and Hanoi. From information gained from scientific workers and others, it was soon evident that Indo-China was an area of big migrations. In one week's stay in that enchanting country, one enormous migration of *Papilio aristheus* (with other species) was seen in the jungle of Annam, and accounts of three other migrations were obtained.

MIGRATIONS IN FRENCH INDO-CHINA.

(1) An account of the *Papilio aristheus* migration has already been published (Fisher, 1939); I would only repeat here that it was of snowstorm proportions and continued for about 20 km., flying S.W. or S.S.W., and took place on 16th April, 1939, at the end of the dry season. *Appias* spp., *Catopsilia crocale* and *Danaus septentrionis* were included in the flight.

A French military aviator gave me an account of two migrations that he had seen. He made the very tentative identification from the illustrations in the British Museum (Natural History) handbook on "Butterfly Migrations in the Tropics".

(2) 16th April, 1938 (the same date as the Annam migration of *Papilio hector*, four or five hundred miles away). About 16 km. on the road from Pailin to Battambang, Cochin-China. In clear forest. Following the ditch alongside the road (? a ribbon migration), flying from just about ground level to about 1 metre high, and going south-west. A species resembling *Catopsilia crocale*.

(3) Tonkin, yearly about the end of April or beginning of May, in the rice fields. Great numbers of dark butterflies with light blue spots, flying westwards. Similar to *Danaus septentrionis*.

(4) Mr. Schlemmer, a travelling missionary, was also interested and gave me the following details of a movement he had seen the previous year: End of April or beginning of May, 1937, on the road between Dalat and Saigon (not very far from No. 1), in flat country. Huge masses of white butterflies, might have been *Appias* sp., flying southwards one day between 10 and 11 a.m. Dry weather, at the very end of the dry season. They flew from ground level to one metre up.

An examination of the records of migration in south and south-east Asia given in Williams (1930) shows a great preponderance of movement towards the south during the months of February, March, and April, at the end of the dry season. The new records given above all took place at this time of year and three out of four have a southerly component; thus, the information from a

new source tends to strengthen the idea. The migration numbered (4) in the next section might also be thought to fall into this group.

MIGRATIONS IN SOUTH-WEST CHINA.

I lived for five and a half years in, or near, Chengtu, Szechuan, travelling a good deal in Szechuan Province, and also visiting the Provinces of Kwangsi, Kweichow, Yunnan and Sikang. During this time, butterfly migrations were watched for, and many people, Chinese and Westerners, were asked for any observations they might have made or heard of. In this way, seven records were obtained for the south-west Provinces, and one for Central Hopei in the north-east.

(1) and (2), *Meitan, Kweichow.*

From early times, Chinese cities, and especially county town or "hsien" cities, have kept records of their history, including such natural phenomena as droughts and floods. The historians also seem to have tried to study omens scientifically: records were kept of various odd occurrences believed to be omens, and an attempt was made to correlate them with other happenings of importance to the inhabitants. In the hope that some of these "omens" might include butterfly migrations, I asked Chinese friends to look through "hsien" records for me. Dr. Liu, Director of The National Agricultural Research Bureau's Tea Research Station, earned my gratitude by finding the following very interesting references in the History of Meitan Hsien, in eastern Kweichow. I hope that more such material may come to hand from time to time.

"In 1827 and 1828, there was a bad drought and the people suffered hunger. In 1833 there were swarms of white butterflies in the city (of Meitan) and they all flew away to the south.

"Li Hen-chien, then Magistrate of Meitan, issued a public order saying "Once in the ancient time, there were the disorders of Wan Lün-chang, subsequent to crowds of frogs around the city. Now these white butterflies flying about are probably a bad omen. For the sake of security in our district, we ought to take preventive measures. But when is the best time to do so?"

"In 1862, there were numerous yellow-white (or yellow and white) moths¹ flying to the west continuously and stopping at the Szechuan border. They died, and afterwards there were the Yellow and White Bandits, who entered the Szechuan border."

(3) *Tinghsien, Hobei.*

Mr. Tsi, of the Entomology Department, Nanking University, told me that he remembered having seen, at about the end of July, 1934, a small migration of some forty or more *Lycaenid* butterflies flying westwards at Tinghsien, in Central Hopei. They were flying about three feet from the ground.

(4) *Nanning, Western Kwangsi.*

On 31st March, 1939, I was travelling by car from Nanning to Lungchow, in Western Kwangsi. At 11 a.m., about 43 miles from Nanning and about eight

¹ Chinese language has different words for "butterflies" and "moths," but I cannot guarantee that these words were used in strict accordance with modern systematics. The migrants *could* have been *PIERIDAE*. I have heard the two words used rather indiscriminately.

miles before reaching Sui-lung Hsien, many dark or black butterflies were seen flying to the east or south-east. The day was fairly warm, dull, and with fair intervals. The wind, S. or S.W., light to moderate. The butterflies flew in ones, twos or threes, about ten or fifteen feet from the ground, and fast. There were usually half a dozen in sight. With a long journey before us through bandit country I was only allowed to stop for a few minutes to try and catch specimens, and the butterflies flew so high and fast that I was unable to take any. But their general appearance and manner of flight were those of large SATYRIDAE. The migration continued for about forty-five miles, and lasted until about 4 p.m., always at the same sparse density. Although only between Densities I and II (Williams 1942), the total number over this long front must have been large. Something of the order of a million individuals may have been involved. The landscape in this part of Kweichow is all rolling grassland, with occasional limestone crags and ranges of grassy mountains. The time of year was well on towards the end of the dry season.

(5) and (6), *Yunnan-Kweichow border.*

On 2nd and 3rd May, 1940, Dr. H. L. Richardson was travelling by bus on the main road on a journey from Kunming (Yunnan) to Kweiyang (Kweichow). On 2nd May migrating butterflies were noticed from forty-five to seventy-nine km. (road distances) E.N.E. of Kunming. The direction of flight was sometimes parallel with the road in the direction of the bus, and sometimes across the road from the right, more or less obliquely; allowing for the bends in the road, the general direction of the flight was to the north-east. Weather was sunny with some clouds; wind was not noted, but it was light.

The main migration was of strongly flying butterflies, which, although white, appeared to differ from the "cabbage whites" also seen. There was an impression of a broad dark border or patch along the front edge of the wing, and a black veining of the wings themselves. (Possibly two species, one with each of these characters?) In size they seemed intermediate between small and large cabbage whites, nearer the large than the small. One, flying parallel with the bus on a fairly level road, was flying nearly as fast—say 20 to 25 miles per hour.

Counts were made (data not now available); for many miles, a butterfly would cross the road about once every few seconds, with occasional patches of more, or less, disperse migration.

"Cabbage Whites" were observed during the migration, fluttering around vegetable gardens or weed patches; some also seemed to take part in the migration, though with less speed and determination. The time was late morning, approaching noon.

On 3rd May, the Yunnan-Kweichow border was crossed, and another similar migration, apparently the same species, was observed at the same time of day. At the time the weather was sunny with some cloud becoming overcast and thundery later; wind was light at first from S.W., changing later to E. The migration was observed between the Kweichow border and Pan-Hsien (Puanting) approximately from 390 to 360 km. west of Kweiyang (Road distances). The general direction of the road was from west to east, and the butterflies were flying across it, *i.e.* from south to north. In appearance and numbers they resembled those of the previous day. They seemed indifferent to variation in relief, flying down valleys or up over ridges with about equal frequency.

(7) *Kuanhsien, Szechuan.*

In October 1940 a thin migration of *Pieris melete* and *P. canidia* was watched by me for several days in Western Szechuan. An account of this migration was sent to the *Journal of the West China Border Research Society* (B) 1941, but, being sent to Shanghai for printing, was lost when the Japanese entered the town. In case the *Journal* is not found when the war comes to an end I repeat the information here.

The migration was first noticed in the Min River Valley. On 12th October, 1940, on a walk between Kuanhsien and Nan Yo Miao, about fifteen miles up the river, *Pieris melete* and *P. canidia* were seen to be common, and there was apparently a southerly drift in progress down the valley. The next two days were cold and rainy, and no movement was seen, but in finer weather on the 15th counts were made at Nan Yo Miao, demonstrating a thin migration to the south. The wind, though light (S.-S.W., Force 1-2) was cold, and the butterflies tended to linger in sunny hollows, flying briskly into the wind between them. After two more cloudy days with no observations, on the return walk to Kuanhsien the same down valley drift was observed.

On the 19th we returned to Chengtu by rickshaw across the Chengtu plain, a distance of about 35 miles. The day was fairly warm, sometimes sunny, with very light wind, east by south. A good many autumn butterflies were seen by the road, including the ubiquitous PIERIDAE. A count was made of every *Pieris* seen, and its direction noted. They were far less common than the previous week, but there was an overwhelming preponderance of movement in a southeasterly direction, that is, across the plain and away from the mountains. The butterflies kept close to the ground, flying about 5 m.p.h.; sometimes faster, sometimes slower than the trotting rickshaws; and tending to linger in sunny corners. The density was very thin; it was very seldom that there were two butterflies within sight of one another.

After returning to Chengtu, watch was kept on the butterflies, and the slow drift seemed to continue. On 21st October, counts showed clearly that the movement was still in progress. It had swung round rather more to the east; the butterflies flew at about the same speed and height as before, and were many times observed to rise over trees and houses, rather than to pass round them. After 21st October, no more movements were seen, and the butterflies decreased in number, disappearing in early November.

(8) *Chengtu, Szechuan.*

On 1st June, 1941, the Rev. Walter Small, of the West China Union University, told me that he had at 9 a.m. that morning seen a mass of cabbage butterflies moving from W. to E. across a market garden south of Chengtu City. The butterflies were flying slowly just above the plants, and were alighting on them and on the path, where they were crushed by the feet of passers-by. But the easterly movement was very distinct in spite of its sluggishness, and, two and a half hours later, returning by the same path, very few of the butterflies were seen where previously there had been hundreds. The day was bright and sunny, and there was little wind. (*Pieris rapae* L., almost certainly the species referred to, was unusually numerous in May and June 1941.) A great deal of damage was done to cabbage and kohlrabi in the market gardens round the town, whole fields being skeletonised by the larvae, which could be seen in dozens on every plant.

One other interesting observation was made by Dr. H. L. Richardson on the

Kialing River, which flows into the Yangtse at Chungking. He saw junks of market garden produce, largely cabbages, coming down the river to Chungking, being followed along by fluttering swarms of cabbage butterflies, which flew round them, alighting on the vegetables. Dr. Richardson called this an "induced migration".

CONCLUSIONS.

There is very little information here on which to theorise. Probably its greatest significance lies in its very paucity; migration does seem to occur in China, but on nothing like the massive scale associated with the area farther south.

Williams (1930) suggests that there may be a palaearctic region of migration, extending from Europe (with North Africa) through the Middle East to Japan. If this should be so, as seems very likely, the observations detailed above would neither prove nor disprove its extension through China; the Provinces visited all lie to the south of such a zone, Chengtu (Latitude 31°) being the most northerly point visited, and corresponding with North Africa in latitude; the climate is of the monsoon type with summer rain. In the hope of seeing the end of southerly migrations or the beginning of northerly ones, a close watch was kept on *Pyrameis* and *Colias* species in spring and autumn. *Pyrameis cardui* and *indica*, and *Colias fieldii* (very like *C. croceus*) and *C. hyale* (subsp. *poliographa*) were watched with some attention in the Chengtu region, but no movements were seen. All these species were often common during autumn and spring months, and they were frequently seen during warm days in winter. The *Colias* appeared to breed on the vetch which is a winter crop on the Chengtu Plain, and larvae of *P. indica* were found on nettles in late spring and early summer. The larvae of *P. cardui* were never found. The adults of all four species could be seen at all times of the year, though they were not common in summer, when they could be seen in much greater numbers in the high mountains to the west.

The possibility of an east-to-west migration between the plains and the mountains was not overlooked, but the migration numbered (7) above was the only concrete piece of evidence in its favour. Many of the local birds follow this course, and may be seen on the plains in the winter, but only high in the mountains during the summer. Three species of Redstart, a hawfinch, and some of the wagtails would fall into this category, and it is not unreasonable to imagine that the Lepidoptera might follow the same course. Cabbages and kohlrabi, which only grow in the hills in the summer, are winter and spring crops on the plains, and the sudden increases and decreases in numbers of PIERIDAE may possibly have been due to such migrations, the density of which was so thin that they went unnoticed. The mountains of West China are very steep, and rise very suddenly from the plains; vertical distances of thousands of feet can be attained in very short horizontal distances. It would thus be possible for vertical migration between the plains and the hills to take place in a very short time, and so escape notice altogether.

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NOTES BY E. BURTT, B.SC., F.R.E.S., ON THE HABITS OF A SPECIES OF *OXYPIIUS* (MANTIDAE), AND THE FLIGHT OF THE MALE OF A SPECIES OF *PALOPHUS* (PHASMIDAE)

By Professor G. D. Hale CARPENTER, M.B.E., D.M., F.R.E.S.

THE antics of MANTIDAE are always amusing, and the following observations from Mr. Eric Burtt, B.Sc., F.R.E.S., are worthy of record. The use of the wings in flight by male PHASMIDAE is, I understand from Dr. B. P. Uvarov, not too well established, and Mr. Burtt's observations on this point are also quoted.

Note 1.

"Tinde, Lohumbo, Tanganyika Territory, 16th Sept. 1943.

"I am sending this observation in case you find it of interest, but the Mantis needs to be observed alive for its interesting features to be duly appreciated, and to do it justice records should be made with a cine-camera. I am sending two specimens, both females. I have only met with five in all. The first was seen early in July, 1942, and the remainder during this dry season. All the specimens were on gravel paths or roads where they are well protected on the speckled surface with its light spots set in browns, like the colour of the insect itself.

"The first example, noted on 2nd July 1942, was a nymph just over a quarter of an inch long. I saw a small dark insect running in short bursts on the ground. When it stopped it appeared to wave massive clubbed antennae in front of it: these were, in fact, the largely developed femora. The adult insect in an attitude of defence sits with head and thorax held almost vertically, and front legs close to the body. The filiform antennae are rapidly vibrated; too rapidly to be clearly distinguished, the limits of the movement being defined as a pair of lines. The extraordinary feature is the display with the front legs, which are stretched out forwards and downwards. The dilated femur is twisted at right angles so that the broad inner surface, mottled in tint and shiny, appears uppermost. The initial part of the movement is done fairly rapidly, but as the limb approaches full extension the movement is very slow and deliberate, giving, as it were, the impression of doing a tremendous stretch with all its strength. The tibia at the same time opens and closes independently, fairly quickly. A full stretch may take about five or six seconds, the tibial movements are at the rate of one a second. Then the limb is withdrawn, at first slowly, then rapidly, and the movement is repeated with the other limb, and so, alternately, perhaps ten or twelve times.

"If the danger seems over the Mantis tries to run away, but if a finger is pointed at it, it again sits up and waves its limbs in defiance. The performance is an amazing one and has to be seen to be believed: even laymen are impressed by it when their attention is drawn to it."

Note 2.

On the use of its wings in flight by the male of a species of *Palophus* (probably *P. episcopalis* Kirby).

Mr. Burt wrote from Tinde, on 5th February, 1945, as follows :—

"I have not seen the insect fly, but have asked the natives about this and they assure me it can, and does, but that it will only fly when the sun is hot. Then it will fly from bush to bush, never very high, and may even fly 200–300 yards." A second letter dated 13th February was as follows : "Another male was brought in here yesterday (it had one hind leg missing) and remained quiescent all day in the laboratory. When, at 4.30 p.m., I went to put it into a box for the night, I noticed that it showed more energy than the previous specimens I have handled, and, to my delight, when I dropped it, it *flew* several feet. This display was repeated several times up and down the laboratory. Then I tried it outside and it flew and circled about, going up to twenty-five feet and finally settled on a tree in the avenue, whence we retrieved it. It flew about one hundred and fifty yards : it was not just a glide as the wings were in motion, a magnificent sight."

I am indebted to Dr. Uvarov for identifying the two Mantids sent by Mr. Burt as a species of *Oxyphilus*.

BOOK NOTICE.

Check-List of the British Lepidoptera with the English name of each of the 2299 species. By I. R. P. HESLOP. 8vo. London (Watkins and Doncaster), 1945. Price 1s. 9d. Pp. 35.

In 1937 Mr. Heslop published his *New Bilingual Catalogue of the British Lepidoptera* and since that time he has been engaged on supplements to it, but because of the war conditions these remain unpublished.

The present *Check-List* epitomises the results of the *Catalogue* and its Supplements.

It claims "for the first time" to present "a complete English nomenclature for the whole of the British Butterflies and Moths, both Macrolepidoptera and Microlepidoptera."

The author admits that in the case of the Microlepidoptera "it is not intended to fix the English nomenclature irrevocably," but claims that in the case of the Macrolepidoptera "the names are of familiar currency and have been largely stabilised as the result of modern works."

CORRELATIONS BETWEEN FLIGHT AND VISION, AND PARTICULARLY BETWEEN WINGS AND OCELLI, IN INSECTS

By H. KALMUS, D.Sc., M.D.

I. INTRODUCTION.

THE general acceptance of the theory of natural selection has not changed such ideas as the correlation between the different parts of an organism and the inter-dependence of form and function. These aspects, however, have tended to be ignored as science became more specialised, and thus interesting problems such as the correlation between locomotion and sense perception have not received the attention they deserve.

The present paper, in which insects only are considered, surveys some taxonomic, morphological, developmental, hereditary and physiological relations between flight and wings on the one hand, and vision and eyes on the other. It does not, of course, aim at completeness in the enumeration of examples, but the material presented will, it is hoped, be sufficient to demonstrate some very general relationships and to draw some unexpected conclusions.

Relations between flight and vision in insects, and especially the joint occurrence or absence of ocelli and wings, has been noted by the systematists in many groups, and some interpretations suggested, but as yet no attempt has been made to survey the problem from the various angles which are necessary for its elucidation. The physiological aspect has been discussed at some length by von Buddenbrock (1937); and his interpretation, together with those of other authors, will be referred to later in this paper. It is perhaps worth noting that relations similar to the one between vision and flight are probably of quite common occurrence; of these the following may be mentioned: sexual dimorphism in the animal kingdom, the negative correlation between complex eyes and antennae in insects (Forel, 1910), and similar correlations between the senses in vertebrates. Those with a bearing on the present problem will be referred to later.

II. VARIABILITY IN FLIGHT AND WINGS.

An individual insect is capable or incapable of flight. For the purpose of this paper, incapacity for flight is taken to be synonymous with lack of wings, although winged insects, both tetrapterous and dipterous, are not necessarily efficient fliers, and in particular they may only take to flight for short periods, *e.g.* most Coleoptera. A family, genus, or even a species may contain both winged and wingless individuals, and the former may differ as regards the size and development of the wings, the wing muscles, and possibly the halteres. Wings may also be reduced in size and venation, and it is often difficult to decide what degree of reduction would make flight impossible.

III. VARIABILITY OF EYES.

Adult insects typically possess two compound eyes and three ocelli on the back of the head. However, most beetles lack ocelli, and in other groups they may be absent, or present singly, in pairs, or in greater numbers, and may occur in various positions on the head.

PROC. R. ENT. SOC. LOND. (A) 20. PTS. 7-9. (OCT. 1945.)

Lack of ocelli is often accompanied by a reduction in facet number of the compound eye, but large compound eyes, covering most of the head's surface, may be found without ocelli, as in the TABANINAE. Members of the same species, genus or family may be ocellate or anocellate, and they may also differ in respect of the facet number of their compound eyes, or, more frequently, in both characters.

IV. CO-VARIATION OF WINGS AND EYES.

The correlation of vision and flight may be investigated, firstly by the study of numerical or quantitative characters of wings and eyes in related forms, *e.g.* wing area and facet number, and secondly by observing the presence or absence of both. Using this latter method, the following situation is revealed.

(a) *The presence and absence of wings and ocelli in systematic insect groups.*

The 23 orders of insects, as listed by Imms (1942), can be grouped according to the presence or absence of ocelli, and wings as follows :

TABLE 1.
Distribution of wings and ocelli in the insect orders.

		Wings		
		Present	Present or absent	Absent
Ocelli	Present	Ephemeroptera Odonata 2	—	—
	Present or absent	Neuroptera Trichoptera	Orthoptera Hemiptera Dermaptera Mecoptera Plecoptera Lepidoptera Isoptera Coleoptera Psocoptera Hymenoptera Thysanoptera Diptera	Thysanura Collembola
		2	12	2
	Absent	—	Embioptera Strepsiptera 2	Protura Anoplura Aphaniptera 3

If the figures in Table 1 representing the numbers of orders are regarded as forming a contingency table we get for $n = 4$, $\chi^2 = 15.4675$ and $P < 0.01$. The coefficient of contingency $C = 0.680$ indicates a strong association between wings and ocelli.

Table 1 shows, in particular, that of the 4 orders where exclusively winged species occur, 2 orders also have ocelli, whereas the species of 2 orders may or may not have them. Of the 5 entirely wingless orders, 3 have only anocellate species and 2 ocellate and anocellate species. No order is completely ocellate and wingless or anocellate and winged, nor is there an order in which all species are ocellate but some wingless. This alone indicates some correlation between

wings and ocelli. The 11 orders in which winged and wingless as well as ocellate and anocellate species occur show that wings have probably frequently been acquired and lost at various later stages in the phylogeny of insects. Consequently possession or lack of ocelli and/or wings forms a frequent criterion for the distinction of lesser systematic units, such as suborders, families, subfamilies and species. Only a very few examples can be discussed in this paper.

The wingless Thysanura and Collembola may be ocellate or anocellate. In the former this character divides the families of the ocellate MACHILIDAE from the anocellate LEPISMATIDAE. As it is not sure whether these apterous insects have ever had winged ancestors, it would seem reasonable to assume that ocelli have developed earlier than wings in the phylogeny of arthropods. This is supported by the fact that some Silurian Trilobites possessed typical ocelli (Handlirsch, 1925) in addition to compound eyes, whereas the first insects, the Paleodictyoptera, which were winged, have been found as late as the Upper Carboniferous strata.

(b) *Sexual dimorphism and heteromorphism in the possession of ocelli and wings.*

Wings and/or ocelli can be present in one sex of an insect species and absent in the other. The anocellate Strepsiptera have winged males and wingless females, whereas the chalcidid *Blastophaga* sp. has winged females

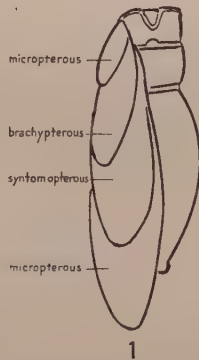


FIG. 1.—Explanation of the terms used in Table 2 for length of wings in the Psocoptera. (after Pearman).

and anocellate wingless males (Handlirsch, 1925). Another parasitic Hymenopteron, *Paracodrus apterogynus* Hal., living in *Agriotes obscurus* L. is ocellate both in the winged male and in the wingless female (Cohen, unpubl.). For the present purpose those families where one sex is dimorphic in some species are most interesting, whereas in others the difference between the sexes is marked. The following data on Psocids, for which I am indebted to Mr. J. V. Pearman, may serve as an illustration. Psocids also show quite clearly the relation of the wing-ocelli question with heteromorphism, sexual dimorphism and perhaps parthenogenesis. The terms in Table 2, micropterous, brachypterous, syntomopterous and macropterous, are explained in fig. 1. Minute wings are smaller than micropterous wings.

Table 2, although demonstrating the reality of the ocelli-wing relation in the Psocids, is difficult of complete statistical treatment. A summary of part

TABLE 2.

Wings and ocelli in some Psocoptera (from data by Pearman, partly unpubl.).

Species	Sex	Ocelli	Fore-wing	Hind-wing
<i>Hyperetes questifalicus</i>	♀, ♂	None	Minute	None
<i>Atropos pulsatoria</i>	♀, ♂	None	Micropterous	None
<i>Lepidilla kelloggi</i>	♀ only	Very small	Brachypterous	Minute
<i>Psoquilla margine-punctata</i>	♀, ♂	None	Brachypterous	Micropterous
	♀	3	Macropterous	Macropterous
<i>Deipnopsocus disparilis</i>	♀, ♂	None	Brachypterous	Micropterous
<i>Embidopsocus enderleini</i>	♀, ♂	None	None	None
	♀	3	Macropterous	Macropterous
<i>Liposcelis</i> spp.	♀, ♂	None	None	None
<i>Psyllipsocus ramburii</i>	♀	3 small	Micropterous	Micropterous
	♀	3 larger	Macropterous	Macropterous
<i>Epipsocus lucifuga</i>	♀	None	None	None
<i>Kolbia quisquiliarum</i>	♀	3	Micropterous	Minute
	♂	3	Macropterous	Macropterous
<i>Terracaecilius freeni</i>	♀, ♂	3 small	Micropterous	Minute
<i>Peripsocus parvulus</i>	♀	3	Brachypterous	Micropterous
	♂	3	Macropterous	Macropterous
<i>Ectopsocus richardsi</i>	♀, ♂	3	Brachypterous	Micropterous
	♀	?	Syntomopterous	Syntomopterous
<i>Reuterella helvimacula</i>	♀	None	None	None
	♂	3	Macropterous	Macropterous
<i>Pseudopsocus rostocki</i>	♀	None	None	None
<i>Nepiomorpha crucifera</i>	♀, ♂	None	None	None
<i>Mesopsocus immunis</i>	♀	None	Minute	Minute
	♂	3	Macropterous	Macropterous
<i>Mesopsocus unipunctatus</i>	♀	None	Minute	Minute
	♂	3	Macropterous	Macropterous
<i>Neopsocus rhenanus</i>	♀	3	Brachypterous	Micropterous
	♂	3	Macropterous	Macropterous

of the data, by grading the development of ocelli and hind-wings, is given in the following contingency table.

TABLE 2B.
Hind-wings.

		++	+	-	
Ocelli	++	8	5	0	13
	+	0	2	0	2
	-	0	4	8	12
		8	11	8	27

Here $\chi^2 = 26.2448$ and $P < 0.001$, while $C = 0.692$, demonstrating a strong association of the two organs.

Among other insect groups where similar conditions prevail, the Thysanoptera are particularly instructive. In this order ocellate and anocellate species and phases occur as well as fully winged, micropterous and apterous

ones. In his monograph on European Thysanoptera, Priesner (1928) writes : " There is probably no other order of insects, showing the correlation between ocelli and wings as clearly as the Thysanoptera " (transl.). Unfortunately neither this modern compilation nor the scattered modern descriptions amounting to some 2000 species provides satisfactory data for statistical treatment. However, Uzel's (1895) classical description of 135 species is an ample demonstration of Priesner's dictum. Table 3, which is compiled from Uzel's description and figures, gives a good idea of the close wing-ocelli relationship in Thysanoptera.

TABLE 3.

Distribution among species of wings and ocelli in the Thysanoptera.
Data from Uzel.

Ocelli	Monomorphic				Dimorphic		
	3 ocelli	2 ocelli	Rudimentary ocelli	No ocelli	Macr. 3 ocelli; brachypt. 2 ocelli	Macr. 3 ocelli; apt. no ocelli	Brachypt. rudimentary ocelli; micr. no ocelli
Wings :							
Monomorphic :							
Macropterous	83						
Micropterous			1	1			
Apterous		1	1	7			
Sexually dimorphic :							
Macropt. ♀, apt. ♂ . .						4	
Macropt. ♀, micropt. ♂ .	1						
Macropt. & brachypt. ♀, apt. ♂	4		1				
Brachypt. ♀, micropt. ♂ .							1
Dimorphic :							
Macropt. & brachypt. ♀ .	1		1		1		
Macropt. & brachypt. ♀ & ♂	1		1				
Macropt. & micropt. ♀ .	1						
Macropt. & apt. ♀ . . .	2		1				
Trimorphic :							
Macropt., brachypt. & micropt. ♀	1						

(c) *Wings and ocelli in aphids.*

In his book on the British aphids Theobald (1926) states that " ocelli do not seem to occur in the apterae whereas the alate viviparous females as well as the alate males have medium and lateral stemmata."

Other co-variations are found between sensory and motor apparatus, *e.g.* in many aphid species the alates have larger compound eyes, better developed chemical organs and richer cuticular structures than the apterous forms. Thus the loss of wings and ocelli of the sedentary and mostly parthenogenetical forms appear again as a partial feature of a more general phase difference, possibly also brought about by neoteny. This in turn is determined by environmental factors. It has been known for many years (Marcus, 1923) that the length of the day controls the phase changes of some aphid species.

(d) *Eyes, ocelli and wings in the castes of social insects.*

Of the social Hymenoptera with winged workers (bees, wasps) there is no marked difference between the ocelli and wings of workers and females, but males (drones) frequently have larger compound eyes than either. However, in the ants, the wingless castes (workers and soldiers), generally have smaller compound eyes than the sexual forms, and also differ from them in being anocellate. There are many references to this in the literature (Donisthorpe, 1927).

In his monograph on the termites from the Australian region Hill (1942) lists 193 species, 8 subspecies and 1 variety. Of these, he describes 137 in the winged adult and soldier castes, 15 in the winged adult caste, 50 in the soldier caste only. Not a single species is recorded where the soldiers have ocelli (or compound eyes) while the winged adults have none; most species have ocellate adults and anocellate soldiers. Among the 137 species where both castes are known, 121 have anocellate soldiers and ocellate adults, 5 are ocellate and 9 anocellate in both castes, while 2 species have either ocellate or anocellate winged adults. No species has ocelli in the soldiers and none in the adults.

Most soldiers not only lack ocelli, but compound eyes also, and even if both types of eyes are present in a soldier, they are smaller than in the winged sexual forms. The phylogeny of this condition was presumably as follows.

If it is assumed that Termites are descendants of winged and ocellate casteless ancestors, it would appear that among the Australian species none has lost the ocelli in the winged adult before it has lost it in the soldier. Five species of *Calotermes* have not lost but only reduced the ocelli in the soldiers, 121 species have lost them in this caste but retained them in the winged sexual forms, and 9 species, mostly *Stolotermes*, have lost them altogether.

(e) *Wing and eye mutants in Drosophila.*

The possession and perfection of eyes and wings and their distribution among insects have so far been considered as final properties of individuals without much regard to their genetical basis or development. This will be considered in the following sections. For a genetical analysis *Drosophila* seems to provide the only material.

In *D. melanogaster* a sex-linked recessive mutant "ocelliess" has been described (Bridges & Brehme 1944) which causes the non-development of the three frontal ocelli and slightly reduces the size of the compound eye, but does not affect the wings.

Another sex-linked recessive, "white," causes white eyes and ocelli instead of red ones, again without affecting the wings. It also slightly decreases facet number. An autosomal recessive, "reduced ocelli" removes the colour entirely from the ocelli. Sometimes the ocelli are completely absent, and the mutant also roughens the surface of the compound eyes.

The autosomal recessive "eyeless" greatly reduces the area and facet number of the compound eyes and the optic ganglia without affecting ocelli or wings. "Eyeless dominant," on the other hand, may cause a reduplication of ocelli or antennae on an enlarged head. "Small eye," a sex-linked recessive, reduces the area of the eye and makes it more prominent. The sex-linked dominant "Bar" reduces the facets to a narrow, vertical strip. The autosomal dominant "lobe" makes a nick in the anterior edge of the eye, and also reduces its size.

Of the numerous mutants affecting area, shape and venation of the wings in *D. melanogaster*, only a few need be mentioned here. In the autosomal recessive series "vestigial" the wings and balancers are either absent or reduced to tiny structures, without affecting the optical apparatus; "apterous," is another wingless mutant; the autosomal recessive "dump" truncates the wings obliquely and reduces their length by a third. "Tiny wing" reduces the wing area. The autosomal recessive "tetraltera" causes the development of haltere-like wings, while in "tetrapter," "bithorax" and "bithoraxoid" the balancers are winglike. Several mutant genes cause abnormal wing position, presumably by affecting the wing muscles, e.g. "aeroplane," in which the wings are spread out and the balancers are drooped, "roof," which causes the wings to droop at the sides, and "elbow," which bends the wings and reduces the size of balancers and alulae.

In view of the great number of genes affecting eyes and wings in *D. melanogaster*, it is not surprising that there are some which affect both. Frequently a roughening of the eye is associated with defects in the wings, as in "facet," "rubroid," "rough wing," "short wing" in which the eyes are small, "polyphene," "jagged" and "expanded," "bulge" and "goggles," which both increases the facet number and eye area, and also affect the wings.

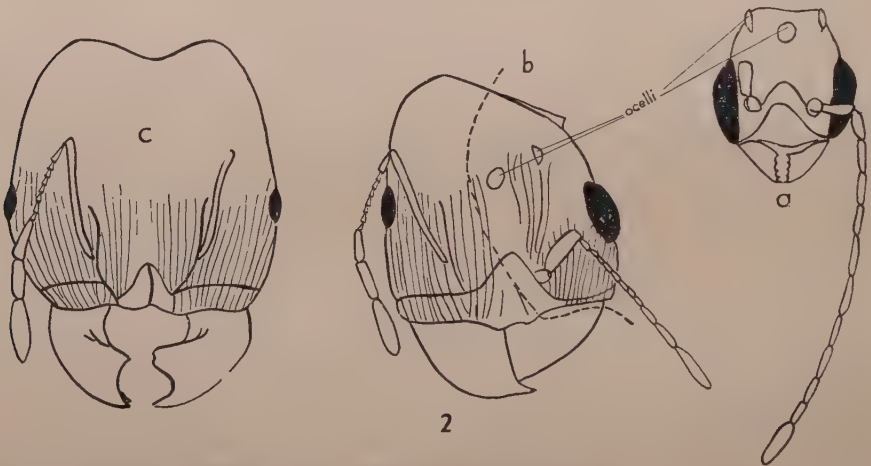


FIG. 2.—Heads of (a) a male and (b) a dinergatandromorph and (c) a soldier of *Pheidole pallidula*. The dotted line in (b) represents the border between male and soldier tissue (after Vandel, modified).

The interaction of wing and eye mutants in *D. melanogaster* has not been extensively studied, but papers by Margolis (1935) show that the wing-reducing gene "vestigial" causes a small but significant additional decrease in the facet number of "Bar" flies at various temperatures. This is probably affected by a slight increase in length of the period in pupal development, in which the gene "Bar" is inhibiting the multiplication of facets.

While it would be incorrect to assume from the above pleiotropic effects that a particular affinity between eye and wing effects exists in genes, yet they do show that they can be jointly regulated by single genes. It will be shown later that they may also be controlled by identical external (environmental) factors. Some examples of their correlation in development will now be given.

(f) *Wing and eye development in mosaics.*

A study of insect mosaics consisting of parts differing in wingedness and visual apparatus may throw some light on their joint development.

Wheeler (1937) discussed 46 gynergates (mosaic female-workers) of *Cephalotes atratus quadridens* of which a few showed asymmetrical heads with a small worker's eye on one side and a larger female on the other. Fig. 2 (reproduced from Vandel's figure) (ref. in Wheeler, 1937) shows a mosaic between soldier and male of *Pheidole pallidula* with the head of a normal soldier (a), the head of a normal male (b) and a dinergatandromorph. Here it is apparent that the size of the compound eyes and the possession of ocelli is determined by the characters of the local tissue. As the mesothorax and metathorax of this animal were entirely of a soldier character it had no wings. However, other ant mosaics have been described where one side was primarily wingless and the other side bore the marks of two wings, both of which had been lost. Tulloch's (1932) gynergate of the primitive *Myrmecia aberrans* Forel had wings and a larger eye on the "female" side, whereas on the left "worker" side of the thorax there were structures which showed that vestigial wings had been present and a smaller compound eye on the asymmetrical head. These facts indicate that the blastogenic and trophogenic hypothesis of caste determination, which should both affect the whole individual, should be abandoned in favour of one which postulates control by a factor working after fertilisation by means of chromosomal or gene mechanisms in individual tissue cells.

In another ant, *Acromyrmex octospinosus*, ocelli were entirely lacking in a remarkable group of 47 gynergates with heads intermediate between female and worker. Wheeler suggests that this is due either to "a histological disturbance of the pupal integument in the region of the vertical carinae or to a strong ocellus-inhibiting factor (perhaps hormonal) in the worker component (i.e. the rest of the body) of the mosaic." The compound eyes as well as other head structures of some of these gynergates were frequently asymmetrical, the one on the female side being the larger.

Adamson (1940) has described some intercastes in the termites. An individual of *Nasutitermes guayanae* (Holmgren) had a head which was in general soldier-like, but possessed compound eyes and certain other features characteristic of the reproductive caste; the wing buds were somewhat similar to those of a reproductive nymph, except that the pigment approached that of the imago. He also described two soldiers of *Microtermes arboreus* with wing buds and abnormally large vestigial eyes in a pigmented area double the size of the one found in soldiers.

(g) *Hormonal control of eye and wing development.*

The compound character of the lateral eyes and the possession of functional ocelli and fully developed wings are characteristic of adult insects. In holometabolic insects wings and ocelli develop during the pupal stage and are wholly absent in the larvae, but in heterometabolic species both structures develop gradually in the last instars. Thus the absence or reduction of one or of both of them can be explained as a larval feature and the reduced form can then be described as neotenic.

Wigglesworth (1936), working on the bug *Rhodnius prolixus*, distinguishes between larval moulting (ecdysis), and metamorphosis. His experiments show that moulting is caused by an unspecific "moulting hormone," possibly produced by the corpus allatum. This organ also has an inhibitory effect on

metamorphosis in the earlier nymphal stages, but it is not quite clear whether the inhibition is caused by the moulting hormone, though at a different level of concentration, or by a different "inhibitory hormone." In any case removal of the corpus allatum in young instars causes premature metamorphosis as shown in the development of wings and other cuticular structures, whereas implantation of corpora allata from younger to last instar nymphs leads to the production of supernumerary 6th and 7th instar forms, which do not occur naturally. Wigglesworth distinguishes between two successive processes in moulting:—

"(1) the epidermal cells detach themselves from the old cuticle; (2) they lay down the new cuticle." Now if the 2nd process supervenes soon after the first has begun, the form of the cuticle will differ very little from that of the preceding instar; in other words, metamorphosis will be inhibited. If, on the other hand, the laying down of cuticle is delayed, sufficient time will have been given for the formation of the adult organs by regrouping of the epidermal cells and hence metamorphosis will take place. Wings and eyes are largely epidermal products and would thus be expected to follow this pattern. Wigglesworth lists full-grown wings and ocelli among the adult characters of *Rhodnius*, but as most of the operations in his work involved decapitation, no reference is made as to the appearance of ocelli in the artificially matured larvae nor to their suppression in the supernumerary instars.

However, there is another example of eye formation (and perhaps ocelli formation also) being influenced by the removal of the corpora allata. Pflugfelder (1939) extirpated this organ in the stick insect *Dixippus morosus* and thus produced a median eye in the ectoderm of the head. This is a completely new structure, never normally found in the species, but present in related forms. Thus in the neotenic stick insect also, removal of the corpus allatum can release an imaginal potency, namely, formation of a median eye.

(h) *Genetical and environmental control.*

Advocates of blastogenic caste and phase determination have been at variance with the supporters of environmental determination for the last century. It seems now that the problem as originally posed cannot be decided generally, but that there is always some interplay between environmental and genetical factors, with one or the other predominating in the various groups. This also applies to the wing-eye correlation, which, as already mentioned (p. 89), may coincide with phase or caste differences.

The development or lack of development of eyes and wings is undoubtedly part of the genotype in most monomorphic insect species. But from this paper it can be deduced that in the species showing polymorphism of eye and wing characters the development of the different types must be predominantly environmental, and not due to the segregation of genes. This has also been shown in some detail for the Thysanoptera by Hood (1940). Only if the two types are in process of becoming separate species can genetical fixation be expected; but even so it need not be absolute. As has been mentioned, mutant genes (*Drosophila*, p. 89) or extreme external influence such as operations (*Rhodnius*, *Dixippus*, p. 91) may still suppress or even produce wings or eyes where this is not normal. Similarly the joint occurrence or absence of wings and ocelli and similar correlations between the apparatus of flight and vision may be determined in each single species either by environmental circumstances such as light, heat, food supply etc. during development (e.g. in aphids, Marcovits, 1923) or genetically by pleiotropic genes or, more probably, by

so-called switch genes. But their being joined depends on their genetical constitution.

Taking all the evidence together, it appears that the joint development or suppression of ocelli and wings can be effected at many levels of differentiation. It may be genetically fixed (1), as in monomorphic species, where it may work (1a) by a hormonal mechanism, affecting metamorphosis as in *Dixippus* or *Rhodnius*, or (1b) by the action of genes, presumably in the chromosomes of the epidermal cells, as in the mosaics of some social insects and of *Drosophila*. In polymorphic species, on the other hand, the degree of eye and wing perfection in a phase must clearly be determined by environmental factors (2) such as light (aphids), temperature or food supply, though these may act via the hormonal system.

Thus the not uncommon situation arises where a widely occurring relationship—the wing-eye correlation—is brought about by very different combinations of internal and environmental factors, none of which is in universal control. Consequently any hypothesis covering all the facts must be of a very general nature, such as the theory of natural selection. If this is accepted, questions of the following type may arise: what is the selective advantage of ocelli to a flying insect? Or alternatively, what use, if any, are ocelli to an apterous form? These questions can be resolved into an inquiry about the functional relationship between the organs of flight and vision.

(i) *Function of the ocelli in flight.*

The function of the ocelli—whether they perceive images, light intensity or light direction—is controversial, and their rôle may differ in different insects. There is disagreement even as regards their innervation. Bozler (1926) has shown a close connection between the ocelli nerves and the optical tracts in the brain of *Drosophila*, whereas Bugnion (1908) has described the ocellar nerve of *Fulgora maculata*, a hemipteron, as a branch of the antennal nerve. Although some ocelli have a lens and admit more light than the facets of the apposition compound eye (e.g. *Eristalis*, Wolsky, 1930), they appear to be ill-designed for the production of images, for in bees the retina of the ocellus is quite out of focus (Hamann, 1924). Consequently theories based on the assumption that the ocelli are specialised for the perception of distant objects (Kolbe, Hesse, Link, quoted from (1) von Buddenbrock, 1936) or alternatively of very near objects (von Buttel-Reepen, Forel, Packard, quoted from von Buddenbrock, 1937) are not very helpful. In addition most ocelli have a very primitive dioptric apparatus. Hess's (1920) description of light-controlled pigment movements in the ocellus of a dragonfly has also been challenged, and it seems altogether rather unlikely that ocelli can perceive images.

There is better evidence to the effect that ocelli have an influence on the general muscular tonus (phototonus) of insects. Bozler (1926) found that dark-adapted *Drosophila* with no ocelli take longer to commence crawling when suddenly illuminated after dark adaptation than do ocellate animals. He regards the ocelli as auxiliary organs only, working in co-operation with compound eyes. Müller's (1931) experiments on the bee seem to support this interpretation, and it is further supported by the close relation in the development of compound eyes and ocelli mentioned earlier in this paper. Von Buddenbrock (1936) also regards the ocelli as stimulatory organs. He states the general relationship between the possession of ocelli and wings in insects, but mentions exceptions to the rule that good fliers have ocelli, e.g. the TABANIDAE, which

have very large compound eyes, and the SPHINGIDAE, where the superposition eyes would be expected to admit more light when dark adapted than any ocelli. The interpretation of ocelli as tonus-producing organs is paralleled by the similar assumption, held by some investigators, concerning the pineal organ, the median eye of the vertebrates.

As early as 1912 Demoll and Scheuring showed that the visual space covered by the ocelli is in most insects only a fraction of that of the compound eyes. Nevertheless it is conceivable that light from a certain direction, *e.g.* from above, may orientate an insect, especially in flight, or for that matter, a trilobite swimming in the sea. Orientational effects of the ocelli of bees have indeed been demonstrated by Müller (1931). As land insects have no static organs, such a device would safeguard the normal position during flight under a light sky. So one would not expect ocelli in fast night- or dusk-flying insects, *e.g.* in the sphingids, noctuids, or some beetles.

The Tabanids, on the other hand, probably have very good "navigational apparatus" in their halteres (Fraenkel, 1939) which may also provide some muscular tonus (von Buddenbrock, 1936).

Summarising, the ocelli appear to have a dual function in assisting flight in insects: (1) they may produce phototonus, thus facilitating taking to the wing and continuous flight in the air, and (2) they may help to keep the flying insect back upmost under a light sky.

DISCUSSION.

The numerical, developmental, genetical and functional correlations between the apparatus of vision and that of flight in insects, as described in this paper, may become clearer if discussed in the light of certain assumptions, some of which are erroneous.

We might assume that a single gene difference was responsible for the presence or absence of wings and ocelli or for the good or poor differentiation of eyes and wings. This hypothesis can be dismissed on the grounds that a pleiotropic factor (*e.g.* one making an insect apterous and anocellate) would still behave as a Mendelian factor. This has never been found in natural populations; the pleiotropic behaviour of some mutants in *Drosophila* affecting eye and wing characters must be regarded as unconnected with the problem.

Nor can the presence or absence of wings and ocelli in one individual normally be due to two pairs of alleles linked in the same chromosome, because they would soon separate by crossing over.

Consequently there is no conceivable chromosome mechanism which might affect the many co-variant intraspecific differences in wingedness and degree of eye development described in this paper. Moreover a blastogenic determination of such characters is quite impossible in the case of mosaics.

The complexity of the lateral eyes, the possession of ocelli and a full development of wings are all three imaginal characters, and all three organs are largely epidermal structures, formed or perfected during the last instar period in hemimetabolic insects, or during the pupal stage in holometabolic insects. Absence or rudimentary development of any of the three organs can consequently be regarded as a larval character, and one would expect an individual which retains larval characters while becoming sexually active (neotenic) to show less developed eyes, ocelli and wings than in the fully developed phase. Thus neoteny would provide an explanation of the wing-eye relationship when

comparing phase, caste and certain sex differences in a species, and when comparing related species.

More details of the factors controlling wing and eye development are known in a few insects.

Wigglesworth (1936) has shown that the corpus allatum, in addition to controlling hormonally the development of both larvae and adult characters, may also control the maturation of ovaries and testes, probably by the production of some "inhibitory hormone." Bodenstein (1942) has shown that different organ systems may respond differently to the same amount of hormone. Since the concentration increases in the body during the period of hormone release, organ systems possessing different hormone thresholds will begin to respond at different times, provided they have reached a certain stage of preparedness. Thus ova and sperm may begin to mature in an insect before the development of such imaginal characters as wings, compound eyes or ocelli is initiated, and if in a species the hormone level does not rise above the latter's threshold, the larval characters may remain unchanged even though eggs and sperm mature.

The hormone production in turn may be controlled by environmental factors such as food, which has been held responsible for the castes in social insects (but see p. 91), temperature or light. It is well known that the phase of many aphid species is controlled by the period of daily illumination (Marcovits, 1923) and that emergence from the pupae in *Drosophila* (Kalmus, 1938a) and many other insects is controlled by light. The perception of this light stimulus is localised in the anterior end of the *Drosophila* pupa (Kalmus, 1938a). Sexual functions may also depend on illumination, e.g. the egg laying of *Dixippus* is predominantly nocturnal (Kalmus, 1938).

External conditions may affect not only the hormone-producing organs, but also the reacting systems, and will frequently influence both. Only in this way can the mosaics, described on p. 91, be interpreted.

It has been suggested that the castes and phases of insects may differ in the number of chromosome sets they possess, i.e. that they are polyploids. The suggestion is probably inapplicable in this primitive form, but more recent findings of organ polyploidism in insects suggest another explanation, namely that the differences between the phases, castes, and, in part, the components of some mosaics, may be due to varying degrees of polyploidism, e.g. of the epidermal cells, the ocelli-, eye- and wing-forming tissues. It is conceivable that the polyploidy of these organs may in turn be controlled by a hormone.

SUMMARY.

Correlative development of eyes and wings, as mainly demonstrated on ocelli and wings, exists in respect of insect orders, families, genera, species, sexes, phases, castes; it extends even to the body parts of some mosaics. Mutant genes affecting both eye and wing characters are known in *Drosophila*, but gene segregation cannot account for the distribution in polymorphic populations. Eye and wing development is probably controlled hormonally by the corpus allatum, and their suppression may be part of a neotenic development, affecting other organs at the same time. In bringing about this widely distributed eye-wing relationship natural selection appears to have acted in many ways and on greatly differing levels of development and organisation. Thus the same end is achieved by very different means. The selective advantage of ocelli to flying insects probably consists in the production of muscular tonus by these organs and possibly in orientating the flying insect with its back to the sky.

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WING-PATTERN IN LYCAENID LEPIDOPTERA

By B. N. SCHWANWITSCH.

(State University of Leningrad, Leningrad, U.S.S.R.)

THE LYCAENIDAE, one of the largest groups of Rhopalocera, though small sized, exhibit a great variety of colour-patterns, many of them being highly specialised. In a research carried through in Leningrad on material of the U.S.S.R. Academy of Sciences a prototype of the wing-pattern of the LYCAENIDAE has been established and by means of it a number of patterns typical of the family analysed. In the present preliminary communication the most general results of the above work are dealt with.

The main distinction of the prototype of the LYCAENIDAE (fig. 5) from that of the NYMPHALIDAE, SATYRIDAE etc. (4) is the absence of eye-spots. Its

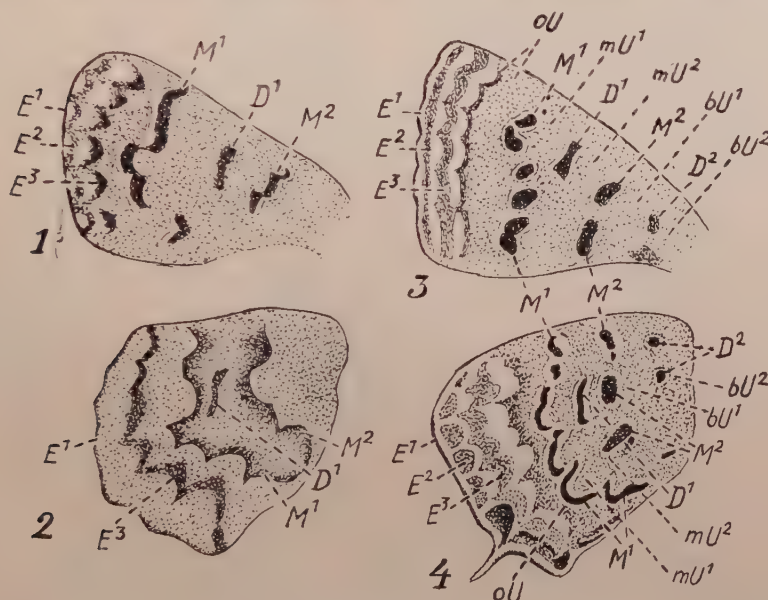


FIG. 1.—*Thecla nippon* Hb. Fore-wing underside. For explanation of lettering, see fig. 5.

FIG. 2.—*Satsuma frivaldskeyi* Ld. Hind-wing underside. For explanation of lettering, see fig. 5.

FIG. 3.—*Chrysophanus virginianus* Edw. Fore-wing underside. For explanation of lettering, see fig. 5.

FIG. 4.—The same, hind-wing.

strial components comprise the system of three similar externae (E^1 , E^2 , E^3), the symmetrical system of two mediae (M^1 , M^2) and the system of two discal stripes (D^1 , D^2). The ocellar system is totally wanting, and the ocellus-like structures typical e.g. of *Lycaena* are nothing but cellular fragments of M^1 and other stripes and never possess white pupils so characteristic of the genuine ocelli (cf. M^1 in fig. 3). No definite basal is has been discovered in the LYCAENIDAE. Besides the strial components there is a system of umbrae

filling up the areas between the striae. It should be emphasised that narrow light interspaces everywhere divide typical umbrae from the stripes, the two sorts of components thus not being in contact. The ocellar umbra (oU) lies between E^3 and M^1 . It is so named because of the nymphaloid eye-spots' series lying in its homologue. The medial umbra fills up the interior of the medial system thus surrounding the first discalis (D^1) and being subdivided by the latter into first and second medial umbrae (mU^1 , mU^2); they correspond to the "Granulatae" of nymphaloid prototype (*loc. cit.*). Likewise the basal umbra is subdivided by the second discalis (D^2) into first and second basal umbrae (bU^1 , bU^2).

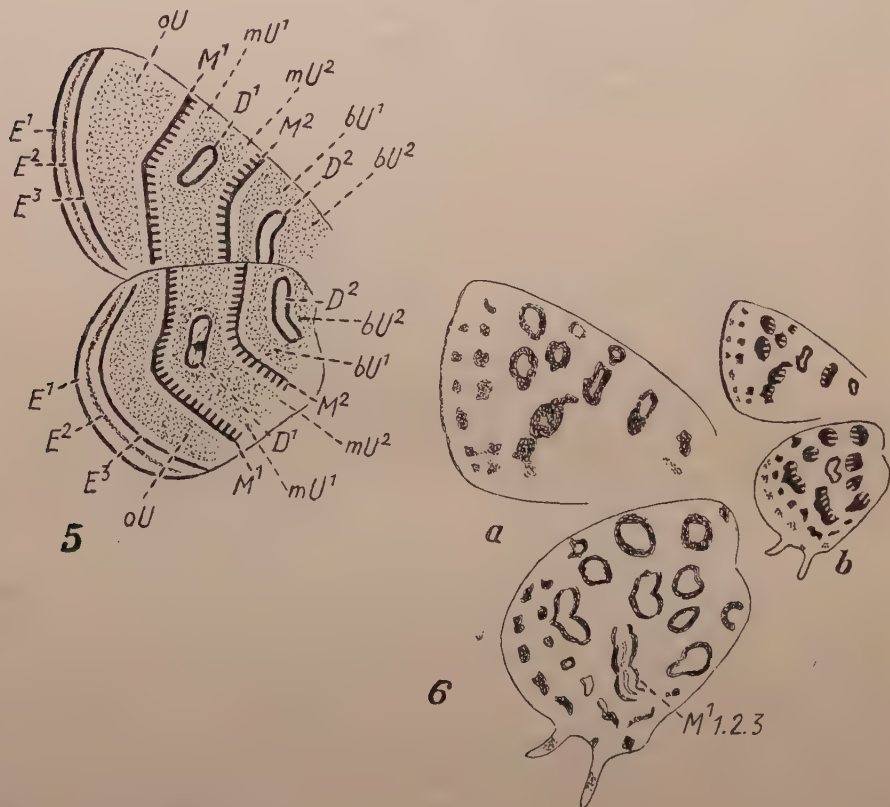


FIG. 5.—Prototype of the wing-pattern of the LYCAENIDAE. Lettering: bU^1 , bU^2 —first and second basal umbrae; D^1 , D^2 —first and second discalia; E^1 , E^2 , E^3 —first, second and third externae; M^1 , M^2 —first and second mediae; mU^1 , mU^2 —first and second medial umbrae; o—ocellar umbra. Stipple marking: black— E^1 and E^3 , densely dotted—umbrae, encircled— D^1 and D^2 , pectinated to the right— M^1 , the same to the left— M^2 .

FIG. 6.—*Cigaritis cilissa* var. *maxima* Stgr. a—underside, b—its diagram in stippling as fig. 5.

To see the typical representation of the prototype in real patterns some three species suffice. On the fore-wing of *Thecla nippon* (fig. 1) D^1 and the systems E^1 , E^2 , E^3 and M^1 , M^2 are present, on the hind-wing of *Satsuma frivaldskyi* (fig. 2) the same components are no less pronounced with the exception of E^2 ,

which is wanting. In *Chrysophanus virginienensis* (figs. 3, 4) there is a rather pronounced complete set of umbrae (oU, mU¹, mU², bU¹, bU²), D² on both wings, E² on hind-wing and postdiscal portion of M² on fore-wing, every one of the enumerated components being scarcely recognisable or totally wanting in *Th. nippon* and *Satsuma*. Thus all the components of the prototype do occur in the representatives of the LYCAENIDAE.

Highly specialised patterns of e.g. *Lycaena*, *Lampides*, *Aphnaeus*, *Hypochrysops*, *Thecla w-album*, *Th. sito*, *Th. saepestriata*, *Thecla betulae* and some others, when analysed by the method of morphological series, proved to be derivations of the above prototype. In this investigation some processes have been recorded which, being met with many times in a number of combinations, seem to be very typical of the variability of pattern in the LYCAENIDAE. The principal of them are cellular fragmentation of stripes, their longitudinal subdivision and the strialisation of umbrae. Fragmentation of e.g. M¹ and M²



FIG. 7.—*Amblypodia azenia* Hew. a—underside, b—its diagram in stippling as fig. 5.

is readily seen in the fore-wing of *Ch. virginienensis* (fig. 3), while in its hind-wing (fig. 4) the stripe E² (continuous in fig. 3) is also broken into cellular fragments. The phenomenon is much more pronounced in *Cigaritis cilissa* (fig. 6), where almost all the stripes have dissolved into unicellular fragments and only a few of the latter as e.g. M¹ 1.2.3 cross over two or three cells. To this process another is added in the mediae and discalia of *Cigaritis*. In the just mentioned tricellular M¹ 1.2.3 the longitudinal subdivision into two halves is evident, while it turns into rings the shorter unicellular fragments. The diagram fig. 6, b where different components are differently stippled explains the morphological composition of the pattern and the numerous dislocations which its fragmented stripes have undergone.

An initial stage of the strialisation of umbrae is to be seen also in *Ch. virginienensis*. The margin of its hind-wing oU has grown somewhat darker than the rest of the component (fig. 4), while on the fore-wing the darkening results in a

formation of a definite stripe (fig. 3). In the remarkable *Amblypodia azenia* (fig. 7) all the umbrae have become stripe-like and do not structurally differ from the majority of somewhat broadened genuine stripes. As both the striae and umbrae have undergone numerous divisions, dislocations and secondary fusions into complex components the morphological interrelations in the "zebroid" pattern which result are very complicated. The derivation of the latter from prototypical forms should not be given here; in the diagram fig. 7, b the established homologies are shown.

In general the described prototype really serves as a basis, giving origin to all the diversity of Lycaenid patterns. On the other hand, the differences of the prototype itself from those of the PAPILIONIDAE (5) and Nymphaloid families (4) are but of secondary importance, and undoubtedly the very essence of the three is the same. Since the indicated families comprise the majority of Rhopalocera we thus advance considerably to the knowledge of the ground plan of the wing-pattern of the whole group, and because of the medial system and first discalis being discovered in Pyralids (3), Arctiids (6), Saturnids (2), Geometrids (1) and some other groups of Heterocera the contours of the ground plan of wing-pattern of all the Lepidoptera begin to stand out.

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